

Effects of urbanization on Odonata assemblages in tropical island streams in San Juan, Puerto Rico

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Abstract. Urbanization has considerable impacts on stream ecosystems. Streams in urban settings are affected by multiple stressors such as flow modifications and loss of riparian vegetation. The richness and abundance of aquatic insects, such as odonates, directly reflect these alterations and can be used to assess urban impacts on streams. The effects of urbanization on odonate richness and abundance on tropical islands is as yet poorly understood. The objective of this study is to identify the effects of urbanization on stream habitat quality and associated odonate assemblages in Puerto Rico. We sampled 16 streams along a rural to urban gradient in the San Juan Metropolitan Area, where each stream was characterized using the Stream Visual Assessment Protocol (SVAP) for Puerto Rico and by analyzing their surrounding land cover. A 100-m segment of each stream was surveyed to assess adult odonate richness and abundance during the rainy and dry seasons. Adults were identified visually, and their abundance was recorded. Favorable local scale factors, like improved habitat quality, as measured with the SVAP, resulted in higher abundances of odonates. However, regional factors such as percent urban cover did not appear to significantly affect richness and abundances of odonates. Overall, our study indicates that odonate assemblages are affected by the loss of habitat integrity, and conservation of tropical odonates may benefit from focusing on local scale factors.

Key words. Caribbean, dragonfly, odonates, riparian vegetation, urban streams

Research Article

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Data Availability Statement:

All relevant data are within the paper.

Introduction

Habitat fragmentation and pollution induced by urbanization influence species richness and abundance (Fahring, 2003; McKinney, 2008). Aquatic environments are especially vulnerable to urbanization, and water quality degradation has been shown to increase with it (Carle et al., 2005; Nagy, 2012; Peters, 2009). Urban streams may share similar manifestations of impacts, such as greater flashiness, increased nutrient concentration, and loss of biodiversity, collectively known as the ‘urban stream syndrome’ (Paul & Meyer, 2001; Walsh et al., 2005). However, different groups of organisms may respond differently to the syndrome, with some increasing their diversity with urbanization (Chironomidae) and others decreasing (Leptophlebiidae) (Bergerot et al., 2011; de Jesús-Crespo & Ramírez, 2011; Ishitani et al., 2003; Urban et al., 2006). This variability in responses makes identifying the impacts of urbanization for specific groups essential.

Odonates are useful habitat quality indicators in a variety of ecosystems (Butler & deMaynadier, 2008; Chovanec et al., 2002; Flenner & Sahlén, 2008; Raebel et al., 2012; Remsburg & Turner, 2009) and have been used to study urbanization

effects on freshwater faunae (Villalobos-Jiménez et al., 2016). The effects of urbanization on odonate assemblages have been studied in the Tropics (Abdul et al., 2017; Monteiro-Júnior et al., 2014), but most of our understanding comes from temperate regions, such as the United States, Germany, Japan, and South Africa (Villalobos-Jiménez et al., 2016). Loss of species, population declines, changes in assemblage composition, and the establishment of invasive species have been identified as some of the effects of urbanization (Córdoba-Aguilar & Rocha-Ortega, 2019; Villalobos-Jiménez et al., 2016). Additionally, stressors such as sewage discharge, alteration of hydrogeomorphology, and loss of vegetation are expected to affect odonate larvae and adults at behavioral and physiological levels (Villalobos-Jiménez et al., 2016).

The effects of urbanization on odonates have not been studied on oceanic islands, even though their faunae are often relatively well known (Meurgey, 2013; Paulson, 2004). Caribbean islands harbor poorly studied species that are endemic to the West Indies (Paulson, 2004; Trapero et al., 2018), and it is unknown whether and if so, to which extent, these species are affected by urbanization. In Puerto Rico, Odonata research commenced back in the 1930s, when the island was mostly agricultural in character (García-Díaz, 1938; Klotz, 1932), with few studies having been published since (Ramírez et al., 2020). Puerto Rico is now a heavily urbanized island, in response to the economy changing from agricultural to industrial in the 1940s (Grau et al., 2003). These drastic changes in land use may have affected and still be affecting odonate assemblages on the island, but they have thus far remained undocumented.

The main objectives of this study are to assess how urbanization affects the structure of Odonata assemblages along a rural to urban gradient and to understand which components of urbanization affect these insects in Puerto Rico. Based on ecophysiological differences (Júnior et al., 2015), we expect species of Zygoptera (conformers) to be more vulnerable to urbanization and habitat alteration, and to be sensitive to changing riparian conditions (Oliveira-Junior et al., 2021). In contrast, we expect species of Anisoptera (heliotherms) to be more resistant to stream habitat modification, due to their higher degree of tolerance to habitat alteration (Remsburg et al., 2008). Based on this, we hypothesize that Zygoptera will be affected more by urbanization and habitat alteration than Anisoptera in Puerto Rico.

Materials and methods

Study organisms

The odonate fauna of Puerto Rico was first studied in the 1930s (García-Díaz, 1938; Klotz, 1932). Since then, the number of species present on the island has been revised by Paulson (1982), Garrison (1986), and most recently by Meurgey (2013) in his review of the dragonflies of the West Indies. It reported 48 species for the island, with Coenagrionidae and Libellulidae being the

most speciose groups (Ramírez et al., 2020). All these species are widely distributed in the West Indies and other parts of the Americas (e.g., *Enallagma coecum* and *Erythrodiplax umbrata*), and include no island endemics (Meurgey, 2013; Ramírez et al., 2020). However, various West Indies endemics, such as *Scapanea frontalis* and *Macrothemis celeno*, are found in Puerto Rico. Overall, dragonflies and damselflies are ubiquitous in the water bodies of the island (Ramírez et al., 2020) and are therefore well suited for ecological studies (Villalobos-Jiménez et al., 2016).

Study area

Our study was carried out in 16 streams in the metropolitan area of San Juan, Puerto Rico (Figure 1). Located in the northeastern part of the island, these study sites are part of three municipalities with 701,366 human inhabitants among them (US Census Bureau, 2012). Most of the area lies within the subtropical moist forest life zone (Holdridge, 1967), has a mean annual temperature of 25.7 °C, and mean annual rainfall of 1,755 mm in its upper parts and 1,509 mm towards the coast (Lugo et al., 2011). The San Juan Metropolitan Area is Puerto Rico's most urbanized zone, thus most of the rainfall (72%) ends up as stream flow (Osterkamp, 2001). Study sites were selected based on land cover, accessibility, and safety.

Environmental characterization

Each stream was sampled twice, once in the rainy season (September–October 2018) and once in the dry season (February–March 2019). Stream habitats were characterized by measuring channel width (in m), air and water temperatures (using a digital thermometer), type of riparian vegetation, and canopy cover. Riparian vegetation was typified by classifying the riparian cover into one of three groups: trees and shrubs, grasses, and none. Each stream was assigned to a group if more than 50% of the cover corresponded to one riparian group. Canopy cover was estimated as a percentage using a spherical concave densitometer. Additionally, the physical condition of the stream habitat was visually evaluated as per the Stream Visual Assessment Protocol (SVAP) for Puerto Rico (Rodríguez & Ramírez, 2014), a rapid method for evaluating the physical conditions of a stream segment.

Odonate sampling

We selected a 100-m segment at each stream and sampled odonates for 30 minutes. During this period, adults were visually identified, and their abundance recorded. If any difficult-to-identify species was encountered, it was captured with aerial nets and identified to genus level using available taxonomic keys (Garrison et al.,

2006, 2010) and to species level by comparisons with our laboratory reference collection. All surveys were conducted on sunny days from 0900 to 1500 hours, as recommended by other Odonata studies (Calvão et al., 2018; Júnior et al., 2015; Monteiro-Júnior et al., 2014; Oliveira-Junior et al., 2019). Diversity studies based on adults have limitations, as observed individuals might be wanderers without a local population. However, previous studies have been successful at using adult Odonata to answer various research questions (Koparde, 2016; Prescott & Eason, 2018; Samways & Steytler, 1996; Sganzerla et al., 2021). The odonate fauna of Puerto Rico is ideal for these types of studies, since there are few species, most are abundant, and contrary to larval stages, are easy to identify (Ramirez et al., 2020).

Land cover analysis

Each study segment was further characterized by analyzing the land cover in a 1-km diameter circle around

each site. Aquatic studies often characterize entire watersheds, but this approach might not be as useful for adult odonates, as these can fly in all directions. Although adult dispersal is not easy to determine and few studies have attempted to do so, Dolný et al. (2014) recorded the maximum dispersal of a medium-sized dragonfly at 1196 m and estimated the probability of it dispersing for more than 1 km at between 13 and 2%. Since the odonate fauna in the island is mostly comprised of Coenagrionidae and Libellulidae (Ramirez et al., 2020), we consider the 1-km radius as appropriate for assessing the area that affects an assemblage. Our study sites were at least 1.1 km distant from each other, with only two sites being separated by 0.90 km from each other. Land cover analyses were completed using ArcGIS Pro(version 2.3). A classified Landsat image of Puerto Rico collated in 2010 (Wang et al., 2017) was used to calculate the percentage of urban development for each study site. We simplified the land cover categories and established 4 classes for our study: urban, forest, herbaceous, and bare (non-vegetated, exposed

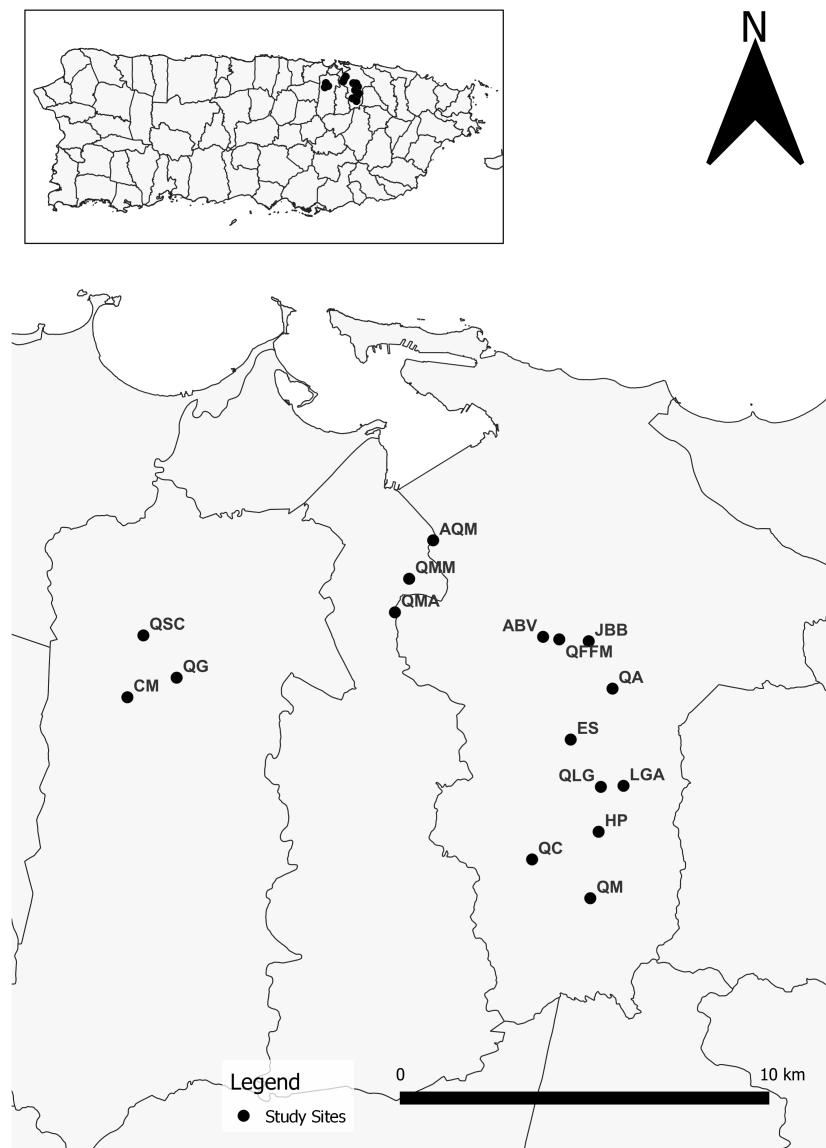


Figure 1. Study sites and site abbreviations within the San Juan Metropolitan Area, Puerto Rico.

terrain). We then extracted the percent urban development for each study site.

Data analyses

Six environmental variables (canopy cover, SVAP, water and air temperatures, percent urban cover, and width) were measured and related to odonate abundance and richness using linear regression analyses. A degree of collinearity was expected in our data set, but given that only six variables were measured, we did not conduct a separate analysis to reduce the number of variables. A PCA was used to visualize the environmental gradient during each season. Data were tested for normality and transformed if necessary (e.g., log or square root). To assess urban and seasonal effects on assemblages, a cluster analysis using Ward's method was used to determine if any groups were formed. This was for each data-set followed by an analysis of similarity (ANOSIM) to determine if groups were significantly different. A similarity percentage (SIMPER) was used to identify which species were responsible for significant group differences. Finally, we used *t*-tests to determine whether habitat quality (SVAP values) or odonate abundances changed between seasons. Analyses were carried out using PAST software (version 3.21) (Hammer et al., 2001). The level of significance for all tests was set at $p < 0.05$.

Results

Odonate assemblages

A total of 3340 specimens were identified, with 14 species (Table 1) within two families being present in both seasons (Coenagrionidae and Libellulidae). The species accumulation curve (Figure 2) showed our sampling effort to be adequate and included most species. Even though the number of observed species is a biased measure, we are confident most species were observed since a first-order jackknife estimator showed that our sampling efficiency was high and the curve was terminally flattening. The most abundant suborder was Zygoptera with 3089 specimens and five species. Although Anisoptera was not as abundant (251 specimens), it was the most speciose suborder with nine species. The dry season resulted in higher abundances (2028 specimens) than the wet season (1312 specimens), but there was high variability, and the difference was not significantly different (t -test = 1.46, $df = 30$, $p = 0.07$).

The most common species were *E. coecum* (2260 specimens) and *Telebasis* spp. (674 specimens) in Zygoptera, and *E. umbrata* (51 specimens) and *M. celeno* (36 specimens) in Anisoptera. Two species of *Telebasis* are present in the area, *T. vulnerata* and *T. dominicana*, but since they are difficult to differentiate visually, we refer to them as *Telebasis* spp. Other species were rarely encountered, for example *S. frontalis* and *Ischnura hastata* were observed only three times and once, respectively.

Table 1. Species and their respective recorded abundances in the wet and dry season at our study streams. * It is not clear which species of *Orthemis* occurs in Puerto Rico, for simplicity, we considered all our specimens as *O. macrostigma*. We also grouped *Telebasis* specimens since two species of *Telebasis* are found in the island (*T. vulnerata* and *T. dominicana*) and are hard to separate visually.

Family/species	Abundance		
	wet	dry	total
Coenagrionidae			
<i>Enallagma coecum</i> (Hagen, 1861)	910	1350	2260
<i>Ischnura ramburii</i> (Selys, 1850)	36	59	95
<i>Ischnura hastata</i> (Say, 1839)	0	1	1
<i>Telebasis</i> spp. (Hagen, 1861)	270	404	674
<i>Protoneura viridis</i> (Westfall, 1964)	12	47	59
Libellulidae			
<i>Erythrodiplax umbrata</i> (Linnaeus, 1758)	12	39	51
<i>Erythrodiplax justiniana</i> (Selys in Sagra, 1857)	2	3	5
<i>Erythemis vesiculosa</i> (Fabricius, 1775)	11	20	31
<i>Perithemis domitia</i> (Drury, 1773)	16	18	34
<i>Orthemis macrostigma</i> * (Rambur, 1842)	7	15	22
<i>Pantala flavescens</i> (Rambur, 1798)	1	5	6
<i>Macrothemis celeno</i> (Selys in Sagra, 1857)	18	18	36
<i>Dythemis rufinervis</i> (Burmeister, 1839)	17	7	24
<i>Scapanea frontalis</i> (Burmeister, 1839)	0	3	3
Tenerals	0	39	39

Stream conditions

Our study streams formed a gradient of conditions from 'degraded' to 'excellent', with SVAP scores ranging from 0.5 ('severely degraded') to 1.8 ('excellent') (Table 2).

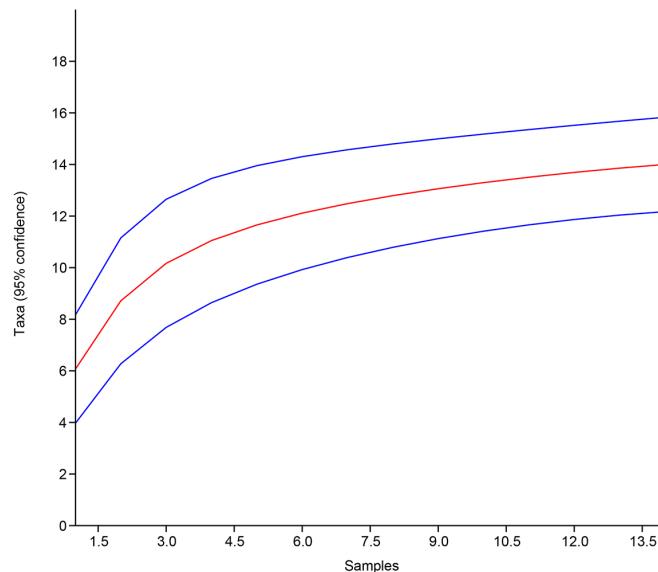


Figure 2. Species accumulation curve for odonate species in the San Juan Metropolitan Area, Puerto Rico. Blue lines indicate 95% confidence intervals.

Table 2. Sites and associated environmental variables. For both seasons average canopy cover is presented as %, Air and Water temperature in °C, and Width in m.

Sites	Coordinates	Average canopy cover (wet)	Average canopy cover (dry)	Air temp. (wet)	Air temp. (dry)	Water temp. (wet)	Water temp. (dry)	Type of canal	Width	Vegetation	SVAP value (wet)	SVAP value (dry)	SVAP value interpretation (wet)	SVAP value interpretation (dry)	Urban cover
Quebrada Gordo	18.38178, -66.16451	1.806667	3.106667	30	26	27.5	24	Channeled	12.3	None	0.7	0.7	Low	Low	0.916849
Canal Marta	18.377, -66.17717	0.16	0.16	36	26.5	30	24	Channeled	6.9	None	0.6	0.6	Low	Low	0.908197
Quebrada Santa Catalina	18.39218, -66.17304	9.953333	10.3	36.5	27	31	25	Channeled	7.3	None	0.6	0.5	Low	Low	0.978142
Quebrada Margarita Arenoso	18.39774, -66.10839	18.53333	32.66	33	34	29	25.5	Natural	7.46	Grasses	1.3	1.4	Regular	Regular	0.761488
Quebrada Margarita Mall	18.40598, -66.10472	12.38	24.42667	29	33	26	27.5	Channeled	5	Grasses	0.8	0.9	Low	Low	0.95614
Afluente Quebrada Margarita	18.41541, -66.09853	52.76667	57.53333	33.5	28	30	26	Natural	4.4	Mixed	1.4	1.2	Regular	Regular	0.940087
Afluente Buena Vista	18.39166, -66.07033	3.973333	7.093333	33.5	32	28.5	26	Channeled	2.6	Grasses	0.9	1	Low	Low	0.904396
Quebrada Frow Fashion Mongil	18.39103, -66.06618	23.64667	37.86	34	29	32	26	Channeled	6.2	None	0.8	0.7	Low	Low	0.861202
Hotel de Perros	18.34377, -66.05617	65.42	64.64	31	26	24.5	25	Natural	6.2	Mixed	1.8	1.8	Very High	Very High	0.324561
Quebrada Los Guanos	18.35479, -66.05556	36.38667	50.34	34.3	28	28	26	Natural	4.18	Mixed	1.3	1.4	Regular	Regular	0.779235
El Señorial	18.36642, -66.06329	30.40667	68.88667	34	26	31	23	Natural	8.94	Mixed	1.2	1.3	Regular	Regular	0.894967
Quebrada Ausubo	18.37891, -66.05252	29.62667	33.7	31	25.5	27	25	Channeled	4.46	Grasses	1	0.8	Low	Low	0.684842
Quebrada Chilcana	18.33701, -66.07327	46.7	61.78	31	27	26	25.5	Natural	2.86	Mixed	1.5	1.7	High	High	0.403084
Quebrada Manuel	18.32745, -66.05834	40.02667	54.06667	31	26	TB	23	Natural	6.2	Mixed	1.8	1.8	Very High	Very High	0.112815
Jardín Botánico Bosque	18.39057, -66.05861	15.84667	22.95333	26	27	24	25	Natural	11.19	Mixed	1	1.4	Low	Regular	0.3954
Los Guanos Arriba	18.35504, -66.04975	69.49333	74.69333	24	28	23	25	Natural	5.09	Mixed	1.4	1.5	Regular	High	0.520833

Scores remained similar between seasons, with most streams being classified as 'severely degraded', five as 'degraded', two as 'good', and two classified as 'excellent' (Table 2). Severely degraded and degraded sites tended to have high organic and inorganic waste (e.g., bottles, tires, food scraps, grass clippings), open canopy, and highly modified or unstable banks. Sites classified as 'good' and 'excellent' had closed canopy cover, less urban waste, were vegetated and had stable banks.

Canopy cover values ranged from 1.8 to 74.7% between both seasons. Air and water temperatures ranged from 24 to 36 and 23 to 32°C, respectively. Channel width ranged from 2.6 to 12.3 m. A PCA (Figure 3) showed that streams with high urban cover had warmer water and air temperatures, open canopies, and lower SVAP values. SVAP scores were not correlated with air and water temperature, or channel width (Table 3). However, a positive relationship between the SVAP and canopy cover was observed and statistically significant (Table 3).

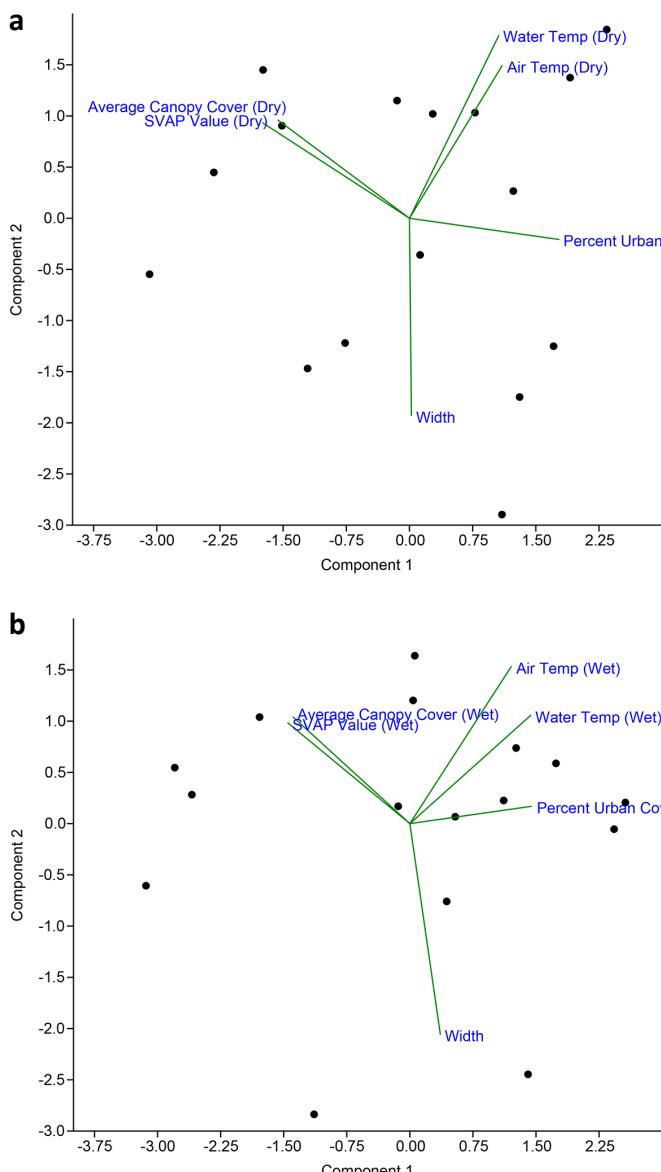


Figure 3. Principal Component Analysis for environmental variables in the dry (a) and wet (b) seasons.

Table 3. Summary statistics for linear regressions against SVAP scores, Anisoptera and Zygoptera abundances. WT = Water temperature (°C), AT = Air temperature (°C), CC = Canopy cover (%), and W = Width (m). Bold values indicate significant regressions at $p < 0.05$.

		Dry		Wet	
		r^2	p -value	r^2	p -value
SVAP	WT	0.05	0.38	0.18	0.09
	AT	0.03	0.56	0.08	0.29
	CC	0.53	0.001	0.69	0.001
	W	0.04	0.48	0.09	0.26
Anisoptera abundance	SVAP	0.001	0.78	0.11	0.2
	WT	0.04	0.44	0.09	0.24
	AT	0.09	0.24	0.001	0.75
	CC	0.001	0.93	0.12	0.18
Zygoptera abundance	W	0.09	0.24	0.09	0.25
	UC	0.06	0.36	0.03	0.53
	SVAP	0.05	0.4	0.02	0.56
	WT	0.02	0.52	0.001	0.74
Zygoptera abundance	AT	0.03	0.53	0.001	0.33
	CC	0.12	0.19	0.02	0.57
	W	0.47	0.003	0.28	0.03
	UC	0.009	0.72	0.003	0.84

Stream condition and odonate assemblage

Cluster analysis and analysis of similarity identified three significantly different groups during both seasons (Figure 4). The groups had different stream memberships during each season, but in both seasons, streams differed in the abundance of *E. coecum* and *Telebasis* spp. Streams with low abundances of these species had low SVAP scores and high urban cover in their surrounding areas. For the dry season, an analysis of variance ($F_{\text{dry}} (2, 13) = 3.93 p_{\text{dry}} = 0.05$) found clustered groups to be marginally different in their SVAP scores while for the wet season they were significantly different ($F_{\text{wet}} (2, 13) = 9.91 p_{\text{wet}} = 0.002$).

Total abundance was positively correlated with the SVAP ($R^2 = 0.36$ and 0.44 for the dry (Figure 5a) and wet (Figure 5b) season, respectively, $p < 0.05$). It is worth mentioning that the abundance values for Quebrada Los Guanos (QLG) were much higher than at all other sites. This site, although exhibiting typical urban stream characteristics, had a well-preserved riparian buffer. When analyzed separately, we found Zygoptera abundance to be positively correlated with the SVAP in both seasons ($R^2 = 0.32, p = 0.02$ and $R^2 = 0.40, p = 0.007$ for the dry and wet season, respectively) while that of Anisoptera was not. In contrast, species richness had no significant correlation with the SVAP in either season. Neither odonate species richness nor abundance were correlated with canopy cover in either season. Even though canopy cover did not directly correlate with richness or abundance it is worth mentioning that SVAP values will in-

crease with canopy cover (Table 3), since a visual canopy estimation forms part of the SVAP. There was no correlation between species richness and abundance and channel width, air temperature, or water temperature. Environmental variables were not significantly correlated with suborder abundances (Table 3), except for channel width, which was negatively correlated with Zygoptera abundance in both seasons ($R^2 = 0.47, p = 0.003$ and $R^2 = 0.28, p = 0.03$ for the dry and wet seasons, respectively).

Urban cover and odonate assemblages

Percent urban cover ranged from 11 to 97% (Figure 6b). In both seasons, a negative correlation was

observed between percent urban cover and SVAP scores (Figure 7). Regressions were not statistically significant, but they show a pattern of qualitatively decreasing habitat condition with increasing urban cover. Groups formed in the cluster analysis did not have significantly different percentages of urban cover (ANOVA: $F_{\text{dry}} (2, 13) = 1.62, p_{\text{dry}} = 0.23$; $F_{\text{wet}} (2, 13) = 2.12, p_{\text{wet}} = 0.16$). In the case of richness (Figure 8) and abundance (Figure 9), no statistically significant correlations were observed (Figure 8a: $R^2 = 0.04, p = 0.44$; Figure 8b: $R^2 = 0.17, p = 0.10$; Figure 9a: $R^2 = 0.04, p = 0.46$; Figure 9b: $R^2 = 0.0002, p = 0.95$). When separating analyses by suborder abundances, no significant correlations were found between these and urban cover (Table 3).

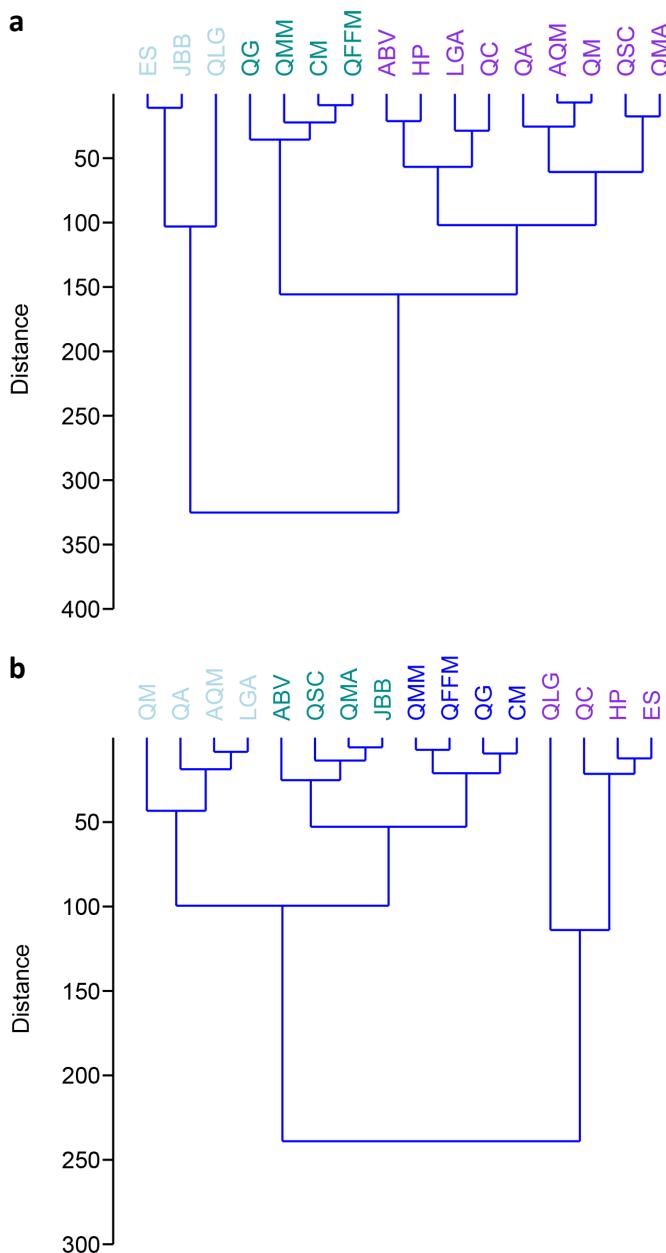


Figure 4. Cluster for dry (a) and wet (b) seasons. A total of 3 groups for each season were formed, and analysis of similarity found the groups significant (Dry $R = 0.80, p = 0.001$; Wet $R = 0.25, p = 0.048$).

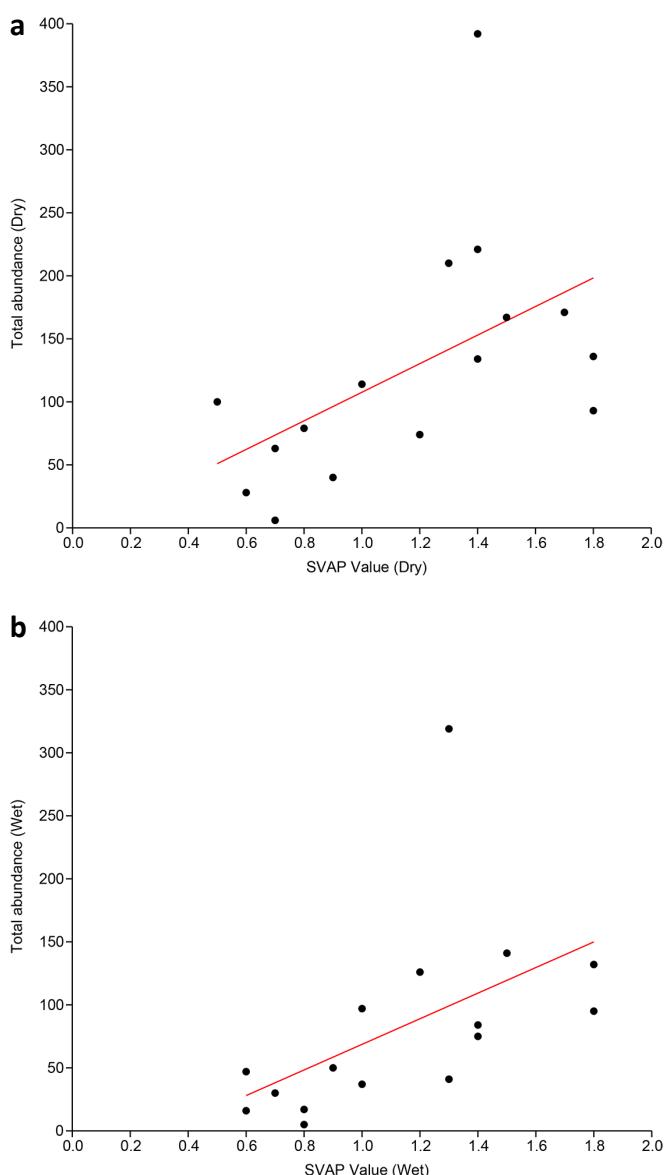


Figure 5. Linear regression for SVAP vs total abundance in the dry (a) and wet (b) season. Black dots represent study sites ($R^2 = 0.36$ and 0.44 for the dry (Figure 3a) and wet (Figure 3b) season, respectively, $p < 0.05$).

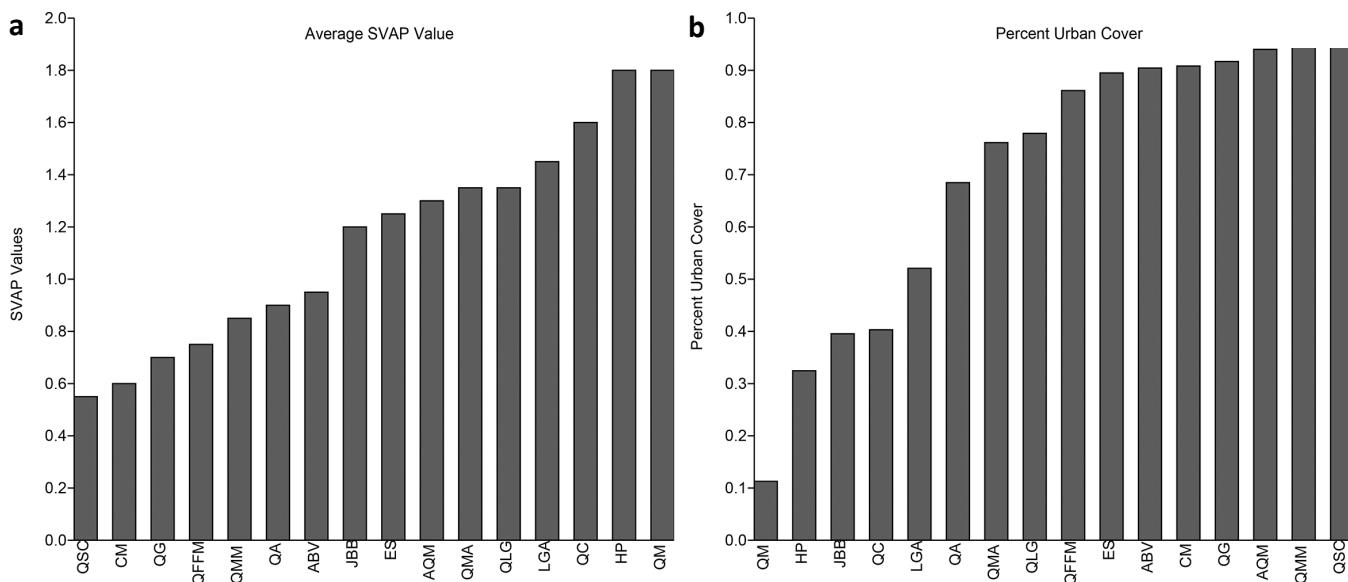


Figure 6. a) Average SVAP score for each site, b) urban cover percentage for each site.

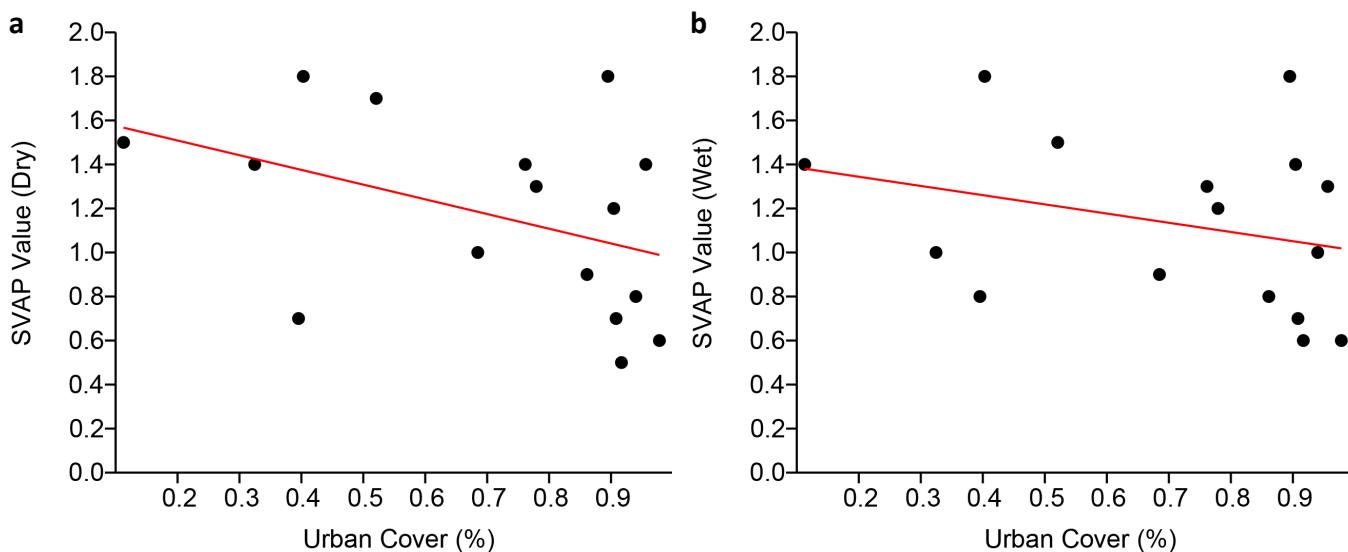


Figure 7. Urban cover percent vs SVAP score for the dry (a) and wet (b) season. Black dots represent study sites.

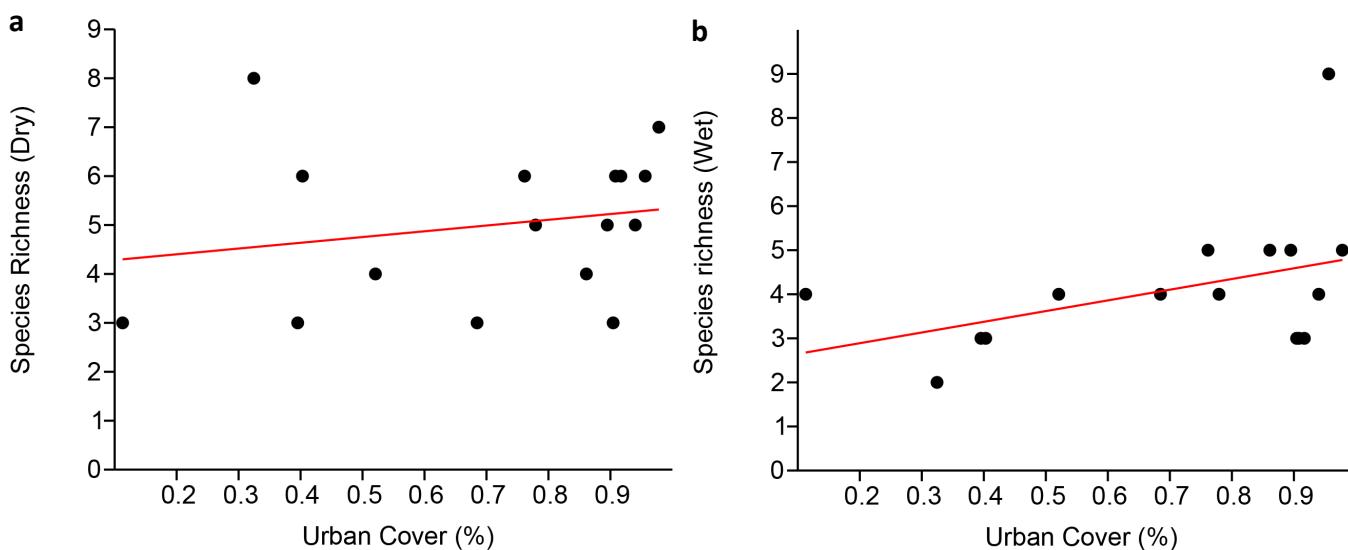


Figure 8. Urban cover percent vs species richness in the dry (a) and wet (b) season. Black dots represent study sites.

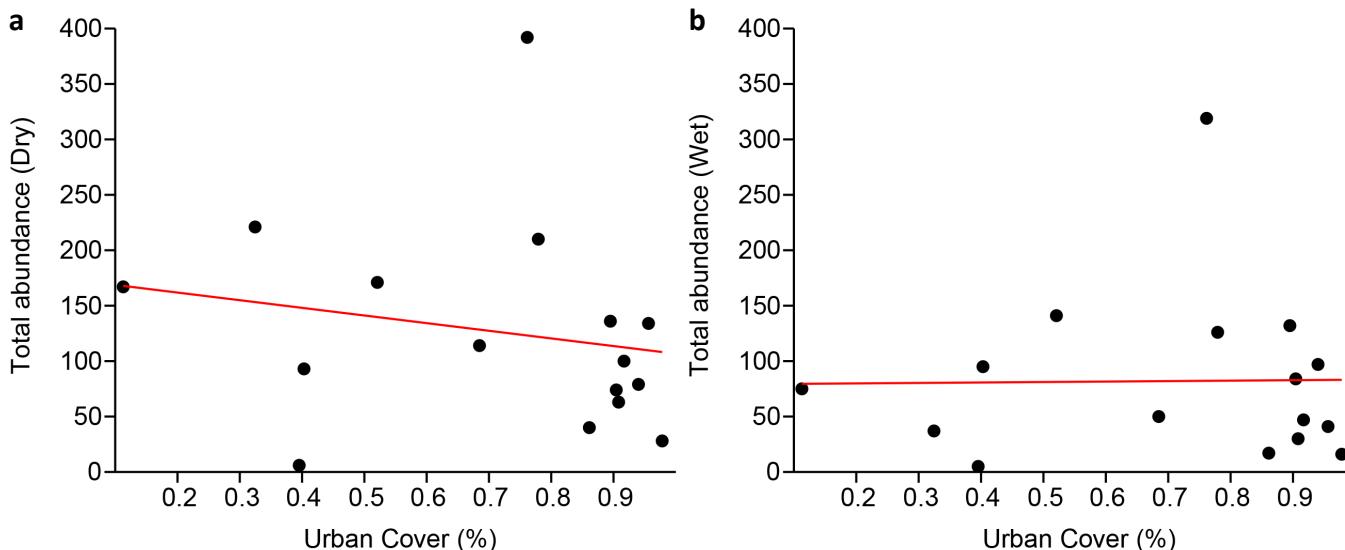


Figure 9. Urban cover percent vs total abundance in the dry (a) and wet (b) season. Black dots represent study sites.

Discussion

Our study in the San Juan Metropolitan Area increases our understanding of how urbanization affects odonates in tropical island streams. Identifying these effects at a regional scale is particularly important, since studies of the group dealt with here have in the past resulted in contrasting patterns for various parts of the world (Villalobos-Jiménez et al., 2016). We expected Odonata assemblages to change in response to the extent of urban cover in their area and to stream habitat condition. Instead, our results suggest that stream habitat condition is mostly responsible for determining odonate assemblages, since streams with low habitat integrity typically have reduced abundances. Similar results have been reported from Brazil, where streams draining pastures had low odonate abundances, but not richness (Calvão et al., 2018). In accordance with our hypothesis, the loss of habitat quality affected Zygoptera more than it did Anisoptera, with stream habitats in better conditions harboring higher abundances of Zygoptera.

The Odonate fauna on the island of Puerto Rico is estimated to be at around 48 species (Ramírez et al., 2020). In our study streams, we identified 29% of the species recorded from the island (14 species), of which most were common species (e.g., *E. coecum* and *E. umbrata*) that are found throughout the island. Our study streams are not ideal habitats for species that either prefer open areas or are largely limited to mountain regions (Ramírez et al., 2020). Thus, species like *Pantala flavescens* and *S. frontalis* were rarely encountered.

Seasonality and its effects on tropical Odonata are poorly known (Corbet, 1999). Available information suggests that seasonality affects the reproductive pattern of the species present, with species with only one generation per year mostly being present in strongly seasonal regions (Gambles, 1960; Kumar, 1972, 1976, 1979). The San Juan Metropolitan Area has a weak seasonal pattern in precipitation, with higher precipitation values being

experienced during the second part of the year, in part due to the hurricane season (Lugo et al., 2011). However, these differences in precipitation do not appear to be a significant factor affecting odonate assemblage composition. In Indian wetlands, Koparde (2016) found significant differences in Zygoptera richness between pre- and post-monsoon seasons, but no significant differences were found for abundance. In our study, we did not observe differences in odonate abundance between seasons. Additionally, stream habitats did not change significantly with the seasons, as is indicated by their similar SVAP scores. Nonetheless, precipitation patterns within the island could be a significant factor influencing odonate assemblages and merit further investigation.

Stream habitat condition is an important factor affecting odonate assemblage structure, with degraded streams hosting different assemblages compared to natural streams (Samways & Steytler, 1996). In our study, compromised habitat conditions (e.g., loss of microhabitats, as measured with the SVAP) were identified as an important variable explaining odonate abundance. Even though other studies have reported higher Libellulidae richness and abundance in urban areas with comparatively low habitat quality values (Ferreras-Romero et al., 2009; Monteiro-Júnior et al., 2014), our results suggest this not to be the case in our study streams. On the other hand, damselflies have been identified as being less tolerant of habitat modifications caused by urbanization (Monteiro-Júnior et al., 2014). Similarly, we observed reduced abundances of Zygoptera in streams with degraded habitats. Riparian vegetation (Carvalho et al., 2013; Monteiro-Júnior et al., 2013) and canopy cover (Remsburg et al., 2008; Steytler & Samways, 1995) influence assemblage composition structure, with damselflies preferring shaded areas and dragonflies preferring sunny areas. For example, in our study, the Quebrada Los Guanos (QLG) had the highest observed abundances, dominated mostly by Zygoptera, and as a result forms an outlier in our data. We believe this could be due to

the fact that the stream, although affected by urbanization, had a well-preserved riparian buffer. Ecophysiological differences between species may result in streams that will be dominated by one suborder, depending on the canopy cover and the availability of spatial heterogeneity. Thus, conserving riparian vegetation and keeping habitats in good condition, mostly in urban streams, might help maintain odonate abundance and richness.

Urbanization alters environmental variables at different scales. We found that habitat characteristics (e.g., segment scale) were the main factors influencing odonate assemblages. Puerto Rico is a densely populated and highly urbanized island, with most of the human population living in the metropolitan area (Martinuzzi et al., 2007). Zygopterans have been found to be less tolerant of contamination caused by urbanization (Monteiro-Júnior et al., 2014). Although we did not measure contamination directly, we observed reduced abundances of Zygoptera in streams with poor habitat conditions. The loss of habitat integrity in streams caused by urbanization on the island clearly influences odonate assemblages. Our results suggest that mid- to low-elevation species on the island may be at greater risk than other species, since most of the urban development on the island is concentrated in coastal areas (Martinuzzi et al., 2007; Wang et al., 2017). Appropriate management practices for different ecosystems are necessary to ensure the conservation of all species on the island. In the case of lotic ecosystems, preserving riparian vegetation and maintaining heterogeneous canopy covers could prove to be effective measures. In our study, no direct correlation was found with riparian vegetation even though it is measured indirectly with the SVAP, and many other studies have identified it as a major influence on odonate assemblages (Carvalho et al., 2013; Monteiro-Júnior et al., 2014; Perron & Pick, 2019; Remsburg et al., 2008). Similar to other studies (Villalobos-Jiménez et al., 2016), our results suggest streams in highly urbanized settings, but with well-preserved habitat structures, may still be functional ecosystems and adequate habitats for many odonate species.

In our study, we found that urban areas maintain a relatively diverse assemblage of Odonata. Odonate abundance was more sensitive than richness to compromised stream habitat conditions and urban cover. Local and regional (e.g., landscape) factors have been identified in other studies as affecting Anisoptera and Zygoptera differently (Ball-Damerow et al., 2014; Nagy et al., 2019). Contrasting with these studies, the regional scale factor we measured does not seem to affect the suborders differently, while local scale factors do. Thus, our data suggests tropical island odonate conservation may benefit from focusing on local factors, especially habitat integrity. As urban areas continue to expand in the Tropics, efficient management practices are needed to protect odonates and other aquatic macroinvertebrates. Practices that include the protection of riparian areas are essential for supporting odonate abundance and the conservation of Zygoptera.

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